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1	Hurricanes and coral bleaching linked to changes in coral recruitment in Tobago
2	
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	_6*
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1

2 Abstract

ACK

3 Knowledge of coral recruitment patterns helps us understand how reefs react 4 following major disturbances and provides us with an early warning system for 5 predicting future reef health problems. We have reconstructed and interpreted 6 historical and modern-day recruitment patterns, using a combination of growth 7 modelling and in-situ recruitment experiments, in order to understand how hurricanes, 8 storms and bleaching events have influenced coral recruitment on the Caribbean 9 coastline of Tobago. Whilst Tobago does not lie within the main hurricane belt 10 results indicate that regional hurricane events negatively impact coral recruitment 11 patterns in the Southern Caribbean. In years following hurricanes, tropical storms and 12 bleaching events, coral recruitment was reduced when compared to normal years (p =13 0.016). Following Hurricane Ivan in 2004 and the 2005-2006 bleaching event, coral 14 recruitment was markedly limited with only 2 % (n = 6) of colonies estimated to have recruited during 2006 and 2007. Our experimental results indicate that despite 15 16 multiple large-scale disturbances corals are still recruiting on Tobago's marginal reef 17 systems, albeit in low numbers.

1 1. Introduction

2

3 An increasing amount of evidence is now accumulating for a direct 4 relationship between global warming and increasing hurricane intensity as well as 5 increasing hurricane frequency (Elsner et al., 2006a, b). Global warming produces 6 significant increases in the frequency of high sea surface temperatures (SSTs) 7 (Hoegh-Guldberg, 1999; Crabbe et al., 2008a), and hurricane winds are strengthened 8 by warm surface waters. Maintaining coral reef populations in the face of large scale 9 degradation and phase-shifts on reefs depends critically on recruitment (Hughes and 10 Tanner, 2000; Coles and Brown, 2007), and the present study set out to test the 11 hypothesis that hurricanes, tropical storms and bleaching events limit the recruitment 12 and subsequent survival of massive non-branching corals. While healthy reefs usually 13 have high numbers of coral recruits and juvenile corals, degraded systems typically 14 have limited numbers of young colonies (Meesters et al. 2001; Smith et al. 2005). An 15 understanding of population dynamics and coral recruitment patterns helps in 16 understanding how reefs react following major disturbances and provides us with an 17 early warning system for predicting future reef health problems. Physical (e.g. 18 sedimentation, salinity, temperature, wave energy, substrate availability) and 19 biological (e.g. predation, density and size of adult colonies, reproductive strategy) 20 factors influence coral reproduction and subsequent recruitment levels (Loya 1976; 21 Cortes and Risk 1985; Szmant 1986; Gilmour 1999; Crabbe et al. 2002; Vermeij et al. 22 2006). Coral bleaching, the loss of colour in the dinoflagellate algae (genus: 23 Symbiodinium) and the coral host, is considered highly deleterious to coral health 24 having negative impacts on growth and reproduction, and making colonies more 25 susceptible to mechanical damage, disease and mortality (Douglas 2003). A number

of external factors can trigger bleaching including elevated temperature, sediment
 smothering, reduced salinity, increased ultra-violet irradiation (Abrego et al., 2008).

3 We have shown previously that growth modelling indicated that hurricanes 4 and severe storms were linked to low coral recruitment in the Caribbean, on the 5 fringing reefs of the north coast of Jamaica near Discovery Bay (Crabbe et al., 2002). 6 and on the barrier reef and patch reefs off the coast of Belize (Crabbe et al., 2008b). 7 We wished to test that hypothesis further and assess whether patterns of coral 8 recruitment in Tobago have been influenced by recent extreme climate-driven events: 9 hurricanes, tropical storms and temperature-induced coral bleaching. Whilst Tobago 10 does not fall within the main hurricane belt the effects of passing storms and 11 hurricanes still influences the island. Hurricanes and storms result in increased 12 rainfall, severe flooding and high levels of terrestrial runoff. High wave energy causes 13 coastal erosion, sediment scouring, mechanical breakage, redistribution of clasts, and 14 loss of substrate. These effects can result in severe damage, or subsequent mortality, 15 to coral colonies and loss of suitable substrate for colonisation (Knowlton et al. 1981; Connell 1997; Connell et al. 1997). The most recent bleaching event in Tobago was 16 17 temperature-induced, beginning in September 2005 and lasting until mid-2006, and 18 affected ≥ 66 % of Tobago's corals (O'Farrel and Day 2005). Many colonies 19 subsequently died (7%) or suffered from partial mortality (33%), whilst the 20 prevalence of coral diseases, especially on the main framework builders Montastrea 21 *faveolata*, increased (Bouchon et al. 2008a and b; Mallela and Parkinson 2008).

In this study we have reconstructed and interpreted historical and modern-day recruitment patterns, using a combination of growth modelling and in-situ coral recruitment experiments, in order to understand how hurricanes, storms and bleaching events have influenced coral recruitment on Tobago's reefs.

1 **2. Materials and Methods**

- 2
- 3 2.1. Study sites
- 4

5 Tobago represents the southern most extreme for modern day framework 6 building coral reefs in the Caribbean. The reefs are characterised by seasonal pulses of 7 river discharge from South America, in particular the Orinoco River during the rainy 8 season (June to December). Riverine inputs include freshwater, sediments and 9 nutrients which result in sub-optimal reef building conditions during the wet season 10 (Bouchon et al 2008b; Mallela and Harrod 2008). As a result Tobago's reefs have 11 evolved, developed and adapted to wide ranging environmental fluctuations which 12 include seasonal pulses of acute, riverine disturbance. For example, in 2008 at a depth of 10m, data obtained from in-situ Star-Oddi TM data loggers revealed that salinity 13 14 ranged from 11.2 to 36.1; temperature ranged from 22.1 to 30.3 °C, and sedimentation rates at 10m depth in 2007 ranged from 0.3 to 15.9 mg cm⁻² d⁻¹. 15

16 Six reef locations: Kariwak, Buccoo, Mt Irvine, Culloden, Little Englishman's 17 Bay and Sisters, were selected along the Caribbean coastline of Tobago (Figure 1). At 18 each site, at a depth of 10m, historical and recent coral recruitment patterns were 19 determined using a combination of methods which included: 1) growth modelling of 20 in-situ colonies, and 2) artificial settlement plates to assess rates of coral recruitment.

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2.2. Growth modelling

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Permanent monitoring transects were established at each site at a depth of
10m. In May and October 2008 coral colonies were haphazardly selected along the

1 transect lines whilst SCUBA diving. The surface area of living, non-branching, 2 scleractinian corals was determined using a series of in-situ measurements. The 3 largest diameter of each colony was measured using a vinyl tape measure, the diameter at 90° to that, and the total circumference of the colony. Colonies that were 4 5 close together, touching, showed signs of partial mortality, fission or fusion were 6 avoided to minimise age discontinuities (Hughes and Jackson 1980). A total of 354 7 colonies were measured and ages subsequently estimated using known growth rates 8 modified where appropriate using a rational polynomial function (RPF) (Carricart-9 Ganivet et al. 2000; Huston, 1985; Crabbe et al. 2002; Crabbe and Smith 2005; 10 Crabbe et al. 2008b; Bardsley, 2009).

11 The year of an individual's recruitment was estimated using the RPF growth 12 model which was based on knowledge of pre-existing growth rate literature (e.g. 3.25 mm y⁻¹ for *Porites astreoides*, 3 mm y⁻¹ for *Siderastrea siderea*) (Dodge and Vaisnys 13 14 1975; Hubbard and Scaturo 1985; Huston 1985; Carricart-Ganivet et al. 2000). Data 15 was taken from sites in the Caribbean at similar depths and visibility to those encountered here, the majority from Huston (1985). For example, a P. astreoides 16 colony of measured elliptical surface area 51.8 cm² was estimated to have recruited 17 18 (and survived) 23 years ago. The modelled changes to the growth rates were similar 19 to those encountered at different sites and similar depths from the references above, 20 and in none of the colonies studied did error levels amount to > 10% of the growth rates measured, equating to a change in estimated recruitment date of $< \pm 2$ years. One 21 22 or two-factor ANOVA was used to compare coral data among sites; ± error values 23 represent standard deviations of the data unless otherwise stated.

1 Prior studies indicate that ceramic settlement plates can be used to accurately 2 assess coral and encruster recruitment (Mallela 2007, Mallela and Perry 2007). In 3 May 2007 ceramic settlement plates (locally made, unglazed clay: surface area 81 4 cm²) were placed at 10m on 6 reefs in Tobago: Kariwak, Buccoo Reef, Mt Irvine, 5 Culloden, Little Englishman's Bay and Sisters Rocks. Plates were positioned in 3 6 orientations in order to mimic natural substrate conditions: exposed / upwards facing (e), cryptic / downwards facing (c), and vertically (v). 18 plates (6 orientation⁻¹) were 7 8 lifted from each site after 6 months and 12 months. 12 month settlement plates were 9 lost at Sisters due to extreme weather conditions. All tiles were screened for coral 10 recruits using a binocular microscope. NAS

11

12 3. Results

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14 Our results indicate that despite multiple large-scale disturbances corals are still recruiting on Tobago's marginal reef systems, albeit in low numbers. Figure 2 15 16 shows the modelled recruitment year for colonies that have recruited to Tobago's 17 reefs since 1980. We identified hurricane, storm and bleaching events which were 18 reported to have had an impact on Tobago's reefs, these included: coral bleaching 19 (2005-2006), Hurricane Ivan (2004), Tropical Storm Isidore (2002), Tropical Storm 20 Bret (1993), and Tropical Storm Danielle (1986). In the early 1980's numbers of the grazing urchin, Diadema antillarum, plummeted in Tobago due to a Caribbean wide 21 22 disease outbreak. There were also wide spread Caribbean bleaching events in 1980, 23 1983, 1990 and 1995, however we were unable to find any records or reports of this in 24 Tobago, consequently these years were not considered bleaching years in our analyses 25 (Figure 2). The results presented here therefore focus on a 25 year period from 1983

- to 2008 on events with reliable records of environmental disturbances on Tobago's
 reefs. Years where there were no reported effects of hurricanes, storms or bleaching
 are from here-in referred to as 'normal' or 'non-event' years.
- 4

5 3.1. Growth modelling

6

7 Between 1983 and 2006 we identified several distinct hurricane, tropical storm 8 and bleaching events (Figure 2), 290 of our colonies also recruited during this period. 9 At all sites, results indicate that in years following hurricanes, tropical storms and 10 bleaching events coral recruitment was significantly limited when compared to 11 normal years, (One-way ANOVA: F = 6.8, p = 0.016, Figures 2 and 3). The peak 12 period for successful recruitment for coral colonies in Tobago occurred between 13 1999-2001, following six normal years, this three year period accounted for 28% of 14 coral colony recruitment since 1983. Following Hurricane Ivan in 2004 and the 2005-15 2006 bleaching event coral recruitment on Tobago's reefs was severely limited with only 2 % (n = 6) of our colonies estimated to have recruited during 2006 and 2007. 16

17 A total of 18 species had recruited since 1983, dominant species included: 18 Colpophyllia natans (3 % of all colonies), Diploria labyrinthiformis (10%), Diploria 19 strigosa (28%), Montastrea cavernosa (11%), M. faveolata (17%), P. astreoides (9%) 20 and S. siderea (10%) (Figure 2). However, following the 2005-2006 bleaching event 21 we observed a distinct drop in the numbers (Figures 2-3) and biodiversity (Figure 2) 22 of coral recruits at all sites with only 4 species present: C. natans, D. strigosa, Favia 23 fragum, and Meandrina meandrites. All sites displayed similar patterns of reduction 24 in coral recruitment following disturbance events.

- 1 3.2. Coral recruitment on settlement plates after the 2005 bleaching event
- 2

3 The number of recent, live recruits observed on settlement plates between 4 2007 and 2008 confirmed findings from our RPF modelling. Limited coral 5 recruitment occurred after 6 and 12 months (Figure 4) with a total of 12 (n = 6 sites) 6 and 17 recruits (n = 5 sites) observed respectively on all plates at all 6 sites. Buccoo 7 had the most recruits after 12 months, with 6 recruits being observed on the 18 plates, 8 all other sites had ≤ 3 recruits on plates after 12 months. Recruits showed a preference for vertical tiles (n = 8 and 13) after 6 and 12 months respectively, with cryptic (n = 09 10 and 4) and exposed (n = 4 and 0) tiles showing limited recruitment. Sisters was the 11 only site where recruits had a preference for exposed tiles (n = 4) after 6 months.

12

13 4. Discussion

14

Our growth modelling and settlement plate experiment indicate that coral 15 16 recruitment declined significantly in years following hurricanes, tropical storms and 17 coral bleaching events. Findings from the settlement plates suggest that recovery can 18 be slow; in this case more than 2 year after the bleaching event Tobago's coral 19 recruitment was still limited in terms of numbers and biodiversity. The main 20 framework builder on Tobago's reefs at the time of this study was M. faveolata 21 (Bouchon et al 2008b), however the live coral cover of this species has fallen 22 dramatically following the 2005 bleaching event and a subsequent disease outbreak of 23 yellow band disease is impacting the remaining population (O'Farrel and Day 2005; 24 Bouchon et al. 2008a; Mallela and Parkinson 2008). In this study, we did not observe 25 recruitment of *M. faveolata* following the multiple disturbance effects of Hurricane

Ivan (2004) and the 2005 – 2006 bleaching event. Limited numbers of juvenile *D. strigosa* and *C. natans* were observed to have successfully recruited post-bleaching.
 These findings could have implications for the future health of Tobago's reefs since
 the continued occurrence of a diverse range of recruits and juvenile corals is essential
 in ensuring healthy, resilient, framework building coral reefs (Smith et al. 2005).

6 Other studies on clear water reefs in the Caribbean have also assessed the 7 effects of hurricanes, storms and bleaching on coral recruitment. In Jamaica, a 8 reduction in coral recruitment of non-branching corals was linked to the effects of 9 storm damage, where increasing storm severity was negatively correlated with coral 10 recruitment (Crabbe et al. 2002). Jamaican non-branching coral recruitment took 1-211 years to return to pre-hurricane levels, and while there was a reduction in numbers of 12 colonies in Jamaican sites in 2006, after the mass bleaching of 2005, there were 13 subsequent increases in 2007 and 2008 (Crabbe, 2009). Reefs of North Jamaica 14 exhibit more rapid recovery than we are currently witnessing on Tobago's reefs 15 following the combined effects of Hurricane Ivan and coral bleaching.

16 In Belize, in 1998 coral populations simultaneously experienced a severe coral 17 bleaching event and Hurricane Mitch. A study of coral recruits (Mumby 1999) found 18 that whilst bleaching alone had no effect on recruitment density or community 19 structure, the combined effects resulted in a 20% reduction of pre-disturbance levels. 20 In Belize only 1% of recruits showed even partial mortality during the 1998 bleaching 21 event. In contrast 66 % of Tobago's coral colonies suffered from bleaching, with an 22 estimated 73 % of C. natans and Diploria spp. dying (Bouchon et al. 2008a). In our 23 study *Diploria* spp. dominated the limited number of recruits from 2004-2006, with C. 24 natans also recruiting in 2006, indicating low levels of recovery for these framework 25 building species. Subsequent growth modelling work in Southern Belize (Crabbe et al.

2008b) also confirm these findings with significantly lower coral recruitment being
 observed in storm and hurricane years.

3

An earlier quantitative study in Tobago (Laydoo 1993) on vertical ceramic 4 plates at 14 m in Buccoo reef recorded mean recruitment levels of 188 m⁻² y⁻¹, this is 5 higher than those observed in this study where coral settlement on vertical plates at 6 Buccoo equated to 103 (\pm SD 81) m⁻² y⁻¹. These observations suggest that 12 to 18 7 months after the bleaching event coral recruitment on Tobago's reefs was still limited 8 9 when compared to recruitment levels in the early 1990's following a series of normal 10 years. Our study also indicates that the majority of recruits showed a preference for 11 vertical orientations, as opposed to horizontal substrates again highlighting the 12 importance of maintaining rugose, varied and complex reef structures.

13

14 Coral reefs that have been undermined can loose their ability to adapt and regenerate (Adger et al. 2005; Crabbe et al 2009). Tobago's reefs historically 15 16 represent some of the most unusual marginal reef systems in the world having 17 successfully developed in the Southern extreme of the Caribbean under the influence of regional riverine influence from two of the world's largest rivers, the Amazon and 18 19 Orinoco. However, these reefs are now facing a series of multiple disturbances 20 simultaneously for the first time. These disturbances include human induced climate 21 change, over fishing, limited herbivory, increased prevalence of coral diseases, 22 pollution from local land-based runoff and deteriorating water quality (Bouchon et al. 23 2008a and b; Burke et al. 2008; Mallela and Parkinson 2008; Mallela and Harrod 24 2008). It is generally accepted that climate change is likely to increase the intensity of 25 hurricanes, storms, bleaching and rainfall events in the region (Bates et al. 2008), the

findings presented here suggest that this in turn may limit successful coral recruitment. Whilst many of the less impacted reefs surrounding the island are still in a coral-dominated state the findings presented here should act as an early warning for coral reef managers. The small numbers of juvenile corals and very limited successful coral recruitment in recent years indicate that Tobago's reefs are currently experiencing a decrease in health which could have long-term implications.

7

8 In conclusion, our results are in agreement with findings from other regions in 9 the Caribbean, indicating that hurricanes, storms and bleaching events do have 10 negative impacts on coral recruitment. Current climate change predictions suggest that 11 the occurrence of such extreme climate driven events will increase. In order to 12 maintain healthy, resilient reefs we must maintain the integrity of all the various reef 13 components.

14

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16

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1 Legends to Figures

2

Figure 1. Map of Tobago, showing the six reef locations selected along the Caribbean
coastline of Tobago in this study: Kariwak, Buccoo, Mt Irvine, Culloden, Little

- 5 Englishman's Bay and Sisters.
- 6

Figure 2. The estimated year of recruitment for all coral colonies in this study 1980-7 8 2006 (solid black line), solid arrows indicate when hurricanes, tropical storms (TS) 9 and bleaching events occurred. Dashed arrows indicate events which may have 10 impacted Tobago's reefs but were not cited in records. The histogram underneath 11 gives the estimated year of recruitment for dominant coral species: Colpophyllia 12 natans (green), Diploria labyrinthiformis (dark grey), Diploria strigosa (yellow), 13 Montastrea cavernosa (light grey), Porites astreoides (white), Siderastrea siderea 14 (black).

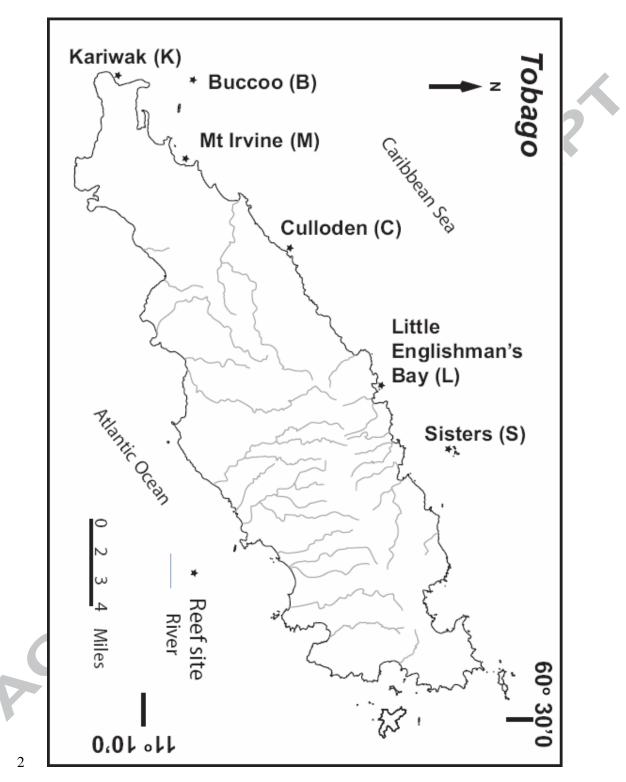
15

Figure 3. Mean number (± 95% confidence intervals) of coral colonies recruiting in
hurricane (H), tropical storm (TS) and bleaching (BL) years (n=6) versus normal
years with no reported incidents (n=18), 1983-2006.

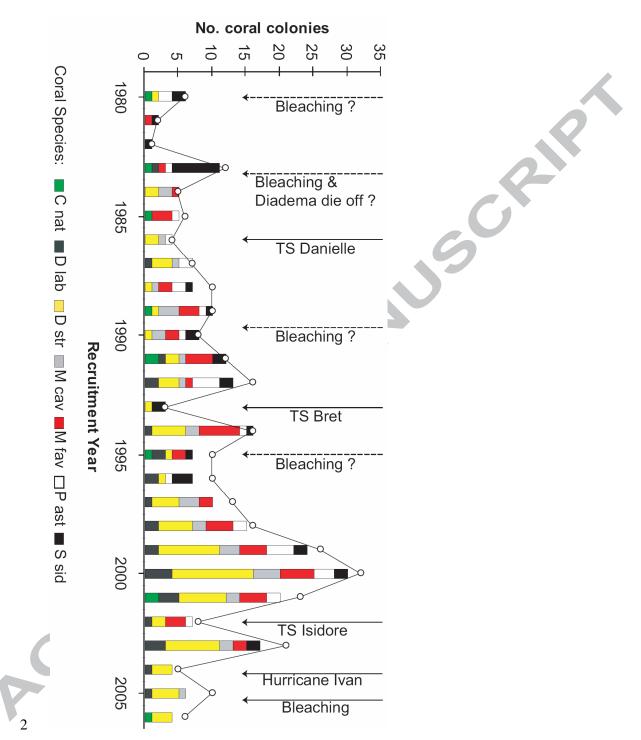
19

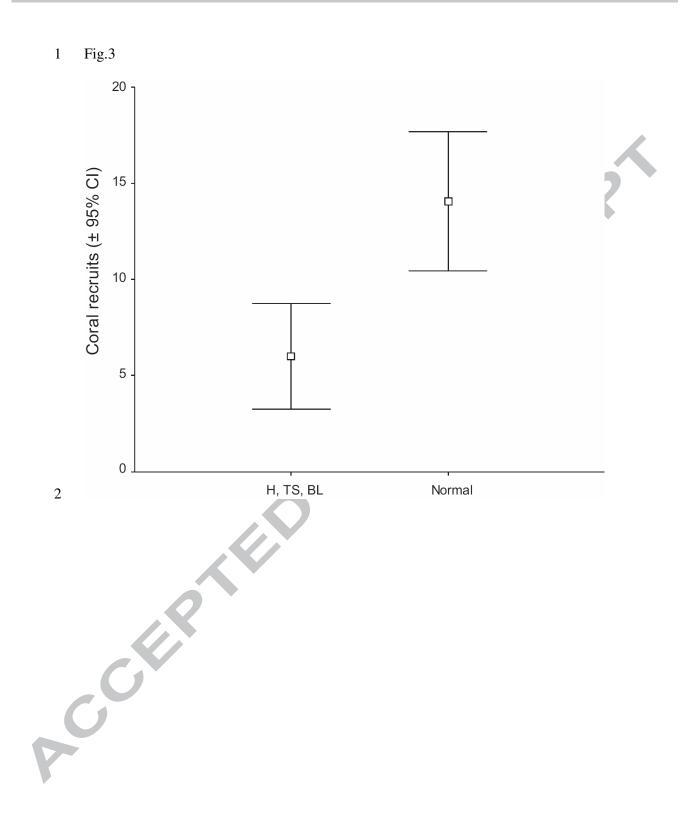
Figure 4. Coral recruitment on settlement plates after the 2005 bleaching event. Box whisker plots detailing coral recruitment after 6 and 12 months on settlement plates at 10m. Reef sites: Kariwak (K), Buccoo (B), Mt Irvine (M), Culloden (C), Little Englishman's Bay (L), Sisters (S). Plates positioned in 3 orientations horizontal exposed (e), horizontal cryptic (c), vertical (v). Note 12 month tiles at Sisters were lost.

1 Fig.1



1 Fig.2





1 Fig.4

